

Locating a Tree in a Reticulation-Visible Network in Cubic Time

Andreas D.M. Gunawan*, Bhaskar DasGupta†, Louxin Zhang‡

Abstract

In phylogenetics, phylogenetic trees are rooted binary trees, whereas phylogenetic networks are rooted acyclic digraphs. Edges are directed away from the root and leaves are uniquely labeled with taxa in phylogenetic networks. For the purpose of evolutionary model validation, biologists check whether or not a phylogenetic tree is contained in a phylogenetic network on the same taxa. Such a tree containment problem is NP-complete. A phylogenetic network is reticulation-visible if every reticulation node separates the network root from some leaves. We answer an open problem by proving that the problem is solvable in cubic time for reticulation-visible phylogenetic networks. The key gadget used in our answer can also allow us to design a linear-time algorithm for the cluster containment problem for networks of this type and to prove that every galled network with n leaves has $2(n - 1)$ reticulation nodes at most.

1 Introduction

How life came to existence and evolved has been a key scientific question in the past hundreds of years. Traditionally, a (phylogenetic) tree has been used to model the evolutionary history of species, in which a node represents a *speciation event* and the leaves represent the extant species under study. Such evolutionary trees are often reconstructed from the gene or protein sequences sampled from the extant species under study. Since genomic studies have demonstrated that genetic material is often transferred between organisms in a non-reproductive manner [3, 19], it has been commonly accepted that (phylogenetic) networks are more suitable for modeling horizontal gene transfer, introgression, recombination and hybridization events in genome evolution [4, 5, 9, 17, 18]. Mathematically, a network is a rooted acyclic digraph with labeled leaves. Algorithmic and combinatorial aspects of networks have been intensively studied in the past two decades [9, 12, 21].

An important issue is to check the “consistency” of two evolutionary models. A somewhat simpler (but nonetheless very important) version of this issue asks whether a given network

*Department of Mathematics, National University of Singapore, Singapore 119076, Singapore.

†Department of Computer Science, University of Illinois at Chicago, Chicago, IL 60607, USA. This work was supported by NSF grant IIS-1160995.

‡To whom correspondence should be addressed. Department of Mathematics, National University of Singapore, Singapore 119076, Singapore. E-mail: matzlx@nus.edu.sg.

is consistent with an existing tree model or not. This motivates researchers to study the problem of determining whether a tree is displayed by a network or not, called the tree containment problem (TCP). The cluster containment problem (CCP) is another related algorithmic problem that asks whether or not a subset of taxa is a cluster in a tree displayed by a network. Both TCP and CCP have also been investigated in the development of network metrics [2, 13]

The TCP and CCP are NP-complete [13], even on a very restricted class of networks [20]. van Iersel, Semple and Steel posed an open problem whether or not the TCP is solvable in polynomial time for reticulation-visible networks [6, 12, 20]. The visibility property was originally introduced to capture an important feature of galled networks [11]. A network is reticulation-visible if every reticulation node separates the network root from some leaves. Real network models are likely reticulation-visible (see [16] for example). Although great effort has been devoted to the study of the TCP, it has been shown to be polynomial-time solvable only for a couple of very restricted subclasses of reticulation-visible networks [7, 20]. Other studies related to the TCP include [15].

In this paper, we make three contributions. We give an affirmative answer to the open problem by presenting a cubic time algorithm for the TCP for binary reticulation-visible networks. Additionally, we present a linear-time algorithm for the CCP for binary reticulation-visible networks. These two algorithms are further modified into polynomial time algorithms for non-binary reticulation-visible networks. Our algorithms rely on an important decomposition theorem, which is proved in Section 4. Empowered by it, we also prove that any arbitrary galled network with n leaves has $2(n - 1)$ reticulation nodes at most.

The rest of the paper is organized as follows. Section 2 introduces basic concepts and notation. Section 3 lists our main results (Theorems 3.1 and 3.2) and gives a brief summary of algorithmic methodologies that lead us to the results. In Section 4, we present a decomposition theorem (Theorem 4.1) that reveals an important structural property of reticulation-visible networks, based on which the two main theorems are respectively proved in Section 5 and Appendix 3 (due to page limitation).

2 Basic Concepts and Notation

2.1 Phylogenetic networks

In phylogenetics, *networks* are acyclic digraphs in which a unique node (the *root*) has a directed path to *every* other node and the nodes of indegree one and outdegree zero (called the *leaves*) are *uniquely* labeled. Leaves represent bio-molecular sequences, extant organisms or species under study. In this paper, we also assume that each non-root node in a network is of either indegree one or outdegree one. A node is called a *reticulation* node if its indegree is strictly greater than one and its outdegree is precisely one. Reticulation nodes represent reticulation events occurring in evolution. Non-reticulation nodes are called *tree* nodes, which include the root and leaves.

For convenience in describing the algorithms and proofs, we add an *open* incoming edge to the root so that its degree is also 3 (Figure 1). A network is *binary* if leaves have degree 1 and all other nodes have degree 3 in the network.

Let N be a network. We use the following notation:

- $\rho(N)$ is the root of N .
- $\mathcal{L}(N)$ is the set of all leaves in N .
- $\mathcal{R}(N)$ is the set of all reticulation nodes in N .
- $\mathcal{T}(N)$ is the set of all tree nodes of degree 3 in N .
- $\mathcal{V}(N) = \mathcal{R}(N) \cup \mathcal{T}(N)$, which is the set of all nodes in N .
- $\mathcal{E}(N)$ is the set of all edges in N .
- For two nodes u, v in N :
 - u is a *parent* of v or alternatively v is a *child* of u if (u, v) is a directed edge in N , and
 - u is an *ancestor* of v or alternatively v is a *descendant* of u if there is a directed path from u to v . In this case, we also say u is *below* v .
- $p(u)$ is the set of the parents of $u \in \mathcal{R}(N)$ or the unique parent of $u \in \mathcal{T}(N) \setminus \{\rho(N)\}$.
- $c(u)$ is the set of the children for $u \in \mathcal{T}(N)$ or the unique child for $u \in \mathcal{R}(N)$.
- $\mathcal{D}_N(u)$ is the *subnetwork* vertex-induced by $u \in \mathcal{V}(N)$ and all descendants of u .
- For any $E \subseteq \mathcal{E}(N)$, $N - E$ is the *subnetwork* of N with the (same) node set $\mathcal{V}(N)$ and the edge set $\mathcal{E}(N) \setminus E$.
- For any subset V of nodes of N , $N - V$ is the *subnetwork* of N with the node set $\mathcal{V}(N) \setminus V$ and the edge set $\{(x, y) \in \mathcal{E}(N) \mid x \notin V, y \notin V\}$.

2.2 The visibility property

Let N be a network and $u, v \in \mathcal{V}(N)$. We say that u is *visible* (or *stable*) on v if every path from the root $\rho(N)$ to v *must* contain u [11] (also see [12, p. 165]). In computer science, u is called a dominator of v if u is visible on v [14].

A reticulation node is *visible* if it is visible on some leaf. A network is *reticulation-visible* if every reticulation node is visible. In other words, each reticulation node separates the root from some leaves in a reticulation-visible network.

The phylogenetic network in Figure 1A is reticulation-visible. Clearly, all trees are reticulation-visible, as they do not contain any reticulation nodes. In fact, the widely studied tree-child networks and galled networks are also reticulation-visible [2, 21].

2.3 The TCP and CCP

Suppression of a node of indegree and outdegree one means that the node is removed and the two edges incident to it are merged into an edge with the same orientation between the two neighbors of it. A tree T' is called a *subdivision* of another tree T if T can be obtained from T' by the suppression of some nodes of indegree and outdegree one in T' .

Consider a binary network N in which each reticulation node has two incoming and one outgoing edges. Thus, the removal of one incoming edge for each reticulation node results in a directed tree. However, there may exist new (dummy) leaves in the obtained tree. For

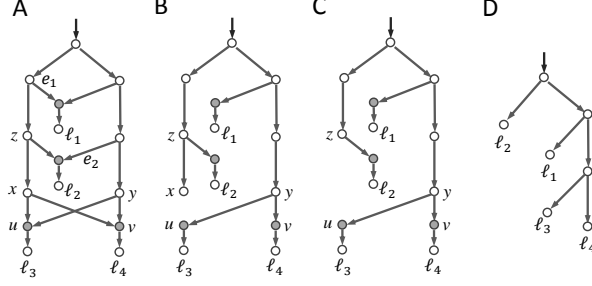


Figure 1: The binary network in panel **A** displays the tree in panel **D** through the removal of four edges $e_1, e_2, (x, v), (x, u)$ (**B**) and the node x (**C**). Here, the reticulation nodes are represented by shaded circles.

example, after removing $e_1, e_2, (x, v)$, and (x, u) in the network given in Figure 1A, we obtain the tree shown in Figure 1B in which x is a new leaf besides the original leaves ℓ_i ($1 \leq i \leq 4$). If the obtained tree contains such dummy leaves, we will have to remove them and some of their ancestors to obtain a subtree having the *same* set of leaves as N .

Definition 2.1 (Tree Containment) *Let N be a network. For each $u \in \mathcal{V}(N)$, d_u^i denotes the indegree of u . N displays (or contains) a phylogenetic tree T over the same taxa (that is $\mathcal{L}(N) = \mathcal{L}(T)$) if $E \subset \mathcal{E}(N)$ and $V \subset \mathcal{V}(N)$ exist such that (i) E contains exactly $d_u^i - 1$ incoming edges for each $u \in \mathcal{R}(N)$, and (ii) $N - E - V$ is a subdivision of T .*

Because of the existence of dummy leaves, V may be nonempty to guarantee that $N - E - V$ has the same set of leaves as T . Note that a binary network with k reticulation nodes can display as many as 2^k trees. The *TCP* is to determine whether a network displays a phylogenetic tree or not.

The set of all the labeled leaves in a subtree rooted at a node is called the *cluster* of the node in a phylogenetic tree. An internal node in a network may have different clusters in different trees displayed in the network. Given a *subset* of labeled leaves $B \subseteq \mathcal{L}(N)$, B is a *soft cluster* in N if B is the cluster of a node in some tree displayed in N . The *CCP* is to determine whether a subset B of $\mathcal{L}(N)$ is a soft cluster in a network N or not.

3 Our Results

Theorem 3.1 (Main Result) *Given a binary reticulation-visible network N and a binary tree T , the TCP for N and T can be solved in $O(|\mathcal{L}(N)|^3)$ time.*

The CCP is another important problem that has a quadratic-time algorithm for reticulation-visible networks [12, pp. 168–171]. Here, we design an optimal algorithm for it. The details of this algorithm are omitted due to page limitation and can be found in Appendix 3.

Theorem 3.2 *Given a binary reticulation-visible network N and an arbitrary subset B of labeled leaves in N , the CCP for N and B can be solved in $O(|\mathcal{L}(N)|)$ time.*

Synopsis of Algorithmic Methodologies The reader may wonder why solving the TCP is hard, as after all N is an acyclic digraph and T is a binary tree. First, it is closely related to the subgraph isomorphism problem (SIP). In general, it is very tricky to find out whether a special case of the SIP remains NP-complete or can be solved in polynomial time. For example, whether or not a directed tree H is a subgraph of an acyclic digraph G is NP-complete, but can be solved in polynomial time provided that G is a forest [8]. Second, there are non-planar reticulation-visible networks. Hence, algorithmic techniques for planar graphs might not be suitable here. Thirdly, the TCP remains NP-complete even for binary networks in which each reticulation node has a tree node as its sibling and another tree-node as its child [20].

The TCP has been known to be solved in polynomial time only for tree-child networks [20] and the so called nearly-stable networks [6]. In a tree-child network, each reticulation node is essentially connected to a leaf by a path consisting of only tree nodes. A simulation study indicates that tree-child networks comprise a very restricted subclass of reticulation-visible networks (Gambette, <http://phylnet.univ-mlv.fr/recophync/>). In a nearly-stable network, each child of a node is visible if it is not visible. Because of the simple local structure around a reticulation node in such a network, one can determine whether or not it displays a phylogenetic tree by examining reticulation nodes one by one. However, any approach that works on reticulation nodes one by one is not good enough for solving the TCP for a reticulation-visible network having the structure shown in Figure 1 if it has a larger number of reticulation nodes above the two reticulation nodes at the bottom. We need to deal with even the whole set of reticulation nodes simultaneously for reticulation-visible networks of this kind.

Our algorithms for the TCP and CCP rely primarily on a powerful decomposition theorem (Theorem 4.1). Roughly speaking, the theorem states that, in a reticulation-visible network, all non-reticulation nodes can be partitioned into a collection of disjoint connected components such that each component has at least *two nodes* if it does not consist of a single leaf. Most importantly, each component *contains* either a network leaf or all the parents of a reticulation node.

The topological property uncovered by this theorem allows us to solve the TCP and CCP by the divide-and-conquer approach: We work on the tree components one-by-one in a bottom-up fashion. In the TCP case, when working on a tree component, we simply call a dynamic programming algorithm to decipher all the reticulation nodes right below it. In the CCP case, a slightly structural complex (but faster) dynamic programming algorithm is used.

4 A Decomposition Theorem

In this section, we shall present a decomposition theorem that plays a vital role in designing a fast algorithm for the TCP and CCP. We first show that reticulation-visible networks have two useful properties.

Proposition 4.1 *A reticulation-visible network N has the following two properties:*

- (a) (Reticulation separability) *The child and the parents of a reticulation node are tree nodes.*

- (b) (Visibility inheritability) *Let $E \subseteq \mathcal{E}(N)$. If $N - E$ is connected and $\mathcal{L}(N - E) = \mathcal{L}(N)$, then $N - E$ is also reticulation-visible.*

Proof (a) Suppose on the contrary there are $u, v \in \mathcal{R}(N)$ such that v is the child of u . Let w be another parent of v . Since N is acyclic, w is not below v and hence not below u . Since w is not a descendant of u , there is a path $P(\rho(N), w)$ from $\rho(N)$ to x that does not contain u .

We now prove that u is not visible on any leaf by contradiction. Assume u is visible on a leaf ℓ . There is a path P' from $\rho(N)$ to ℓ containing u . Since v is the only child of u , v appears after u in P' . Define $P'[v, \ell]$ to be the subpath of P' from v to ℓ . The concatenation of $P(\rho(N), w)$, (w, v) , and $P'[v, \ell]$ gives a path from $\rho(N)$ to ℓ . However, this path does not contain u , a contradiction.

(b) The proposition follows from the observation that the removal of an edge only eliminates some directed paths and does not add any new path from the root to a leaf. \square

Consider a reticulation-visible network N . By Proposition 4.1, each reticulation node is incident to only tree nodes. Furthermore, each connected component C of $N - \mathcal{R}(N)$ (ignoring edge direction) is actually a subtree of N in which edges are directed away from its root. Indeed, if C contains two nodes u and v both of indegree 0, where indegree is defined over $N - \mathcal{R}(N)$, the path between u and v (ignoring edge direction) must contain a node x with indegree 2, contradicting that x is a tree node in N . Hence, the connected components of $N - \mathcal{R}(N)$ are called the *tree-node components* of N .

Let C be a tree-node component of N and $\mathcal{V}(C)$ denote its vertex set. It is called a *single-leaf component* if $\mathcal{V}(C) = \{\ell\}$ for some $\ell \in \mathcal{L}(N)$. It is a *big* tree-node component if $|\mathcal{V}(C)| \geq 2$. The binary reticulation-visible network in Figure 2A has four big tree-node components and five single-leaf components.

By definition, any two tree-node components C' and C'' of N are disjoint. We say C' is *below* C'' if there is a reticulation node r such that C'' contains a parent of r and the child of r is the root of C' .

Theorem 4.1 (Decomposition Theorem) *Let N be a reticulation-visible network with m tree-node components C_1, C_2, \dots, C_m . The following statements are true:*

- (i) $\mathcal{T}(N) = \uplus_{k=1}^m \mathcal{V}(C_k)$.
- (ii) *For each reticulation node r , its child $c(r)$ is the root of some C_i , and each of its parents is a node in a different C_j .*
- (iii) *For each tree-node component C_k ,*
 - (a) $|\mathcal{V}(C_k)| = 1$ *iff* $\mathcal{V}(C_k) = \{\ell\}$ *for some $\ell \in \mathcal{L}(N)$ (i.e. it is a single-leaf component), and*
 - (b) *If C_k is big, either C_k contains a network leaf or a reticulation node r exists such that its parents are all in C_k .*
- (iv) *A big tree-node component C exists such that there are only single-leaf components below it.*

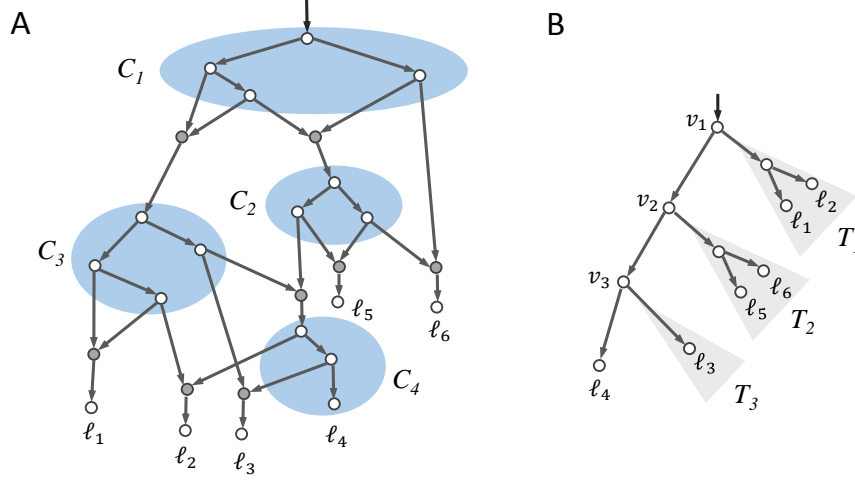


Figure 2: **(A)** A binary reticulation-visible network having 9 tree-node components, of which four (C_1 – C_4) are the big ones. **(B)** A tree for consideration of its containment in the network. When $C = C_4$ is first selected, we focus on the path from the root v_1 to ℓ_4 in the given tree, where $L_C = \{\ell_4\}$, $s_C = 4$ and $d_C = 3$.

Proof (i) The set equality follows from the fact that the tree-node components are all the connected components of $N - \mathcal{L}(N)$.

(ii) Let $r \in \mathcal{R}(N)$. By the *Reticulation Separability* property in Proposition 4.1, $c(r)$ and the parents of r are all tree nodes. Thus, by (i), each of them is in a tree-node component. Furthermore, since $c(r)$ is of indegree 0 in $N - \mathcal{R}(N)$, $c(r)$ must be the root of the tree-node component where it is found.

(iii) (a) Let C be a tree-node component such that $|C| = 1$. Assume $C = \{u\} \subset \mathcal{T}(N) \setminus \mathcal{L}(N)$. Since u is the only non-leaf tree node in C , $p(u) \in \mathcal{R}(N)$ and $c(u) \subseteq \mathcal{R}(N)$. Any leaf descendant of $p(u)$ must be below some child of u . Let $c(u) = \{c_1, c_2, \dots, c_k\}$ be the children of u . Since k is finite and N is acyclic, there is a subset S of i children $c_{k_1}, c_{k_2}, \dots, c_{k_i}$ such that (i) c_{k_j} is not below any node in $c(u)$ for each j , and (ii) each child in $c(u)$ is either in S or below some child in S . For each $j \leq i$, using the same argument as in the proof of the part (a) of Proposition 4.1, we can prove that for each leaf ℓ below c_{k_j} , there is path from $\rho(N)$ to ℓ not containing $p(u)$. Since any leaf below $p(u)$ must be below some child in S , $p(u)$ is not visible. This contradicts the fact that N is reticulation-visible. Therefore, $|C| = 1$ if and only if it is a single-leaf component.

(b) Assume that C is a big tree-node component of N , that is, $|\mathcal{V}(C)| \geq 2$. Let $\rho(C)$ be the root of C . $\rho(C)$ and its reticulation parent are visible on some network leaf, say ℓ . If ℓ is in C , we are done.

If ℓ is not in C , we define $\mathcal{X} = \{r \in \mathcal{R}(N) \mid p(r) \cap C \neq \emptyset \text{ \& } \ell \text{ is below } r\}$. For any $r', r'' \in \mathcal{X}$, we write $r' \prec_{\mathcal{X}} r''$ if r' is below r'' , that is, there is a direct path from r'' to r' . Since $\prec_{\mathcal{X}}$ is transitive, \mathcal{X} is finite and N is acyclic, \mathcal{X} contains a maximal element r_m with respect to $\prec_{\mathcal{X}}$. Let $p(r_m) = \{p_1, p_2, \dots, p_k\}$. Since $r_m \in \mathcal{X}$, we may assume that $p_1 \in \mathcal{V}(C)$. If $p_{k_0} \notin \mathcal{V}(C)$ for some $1 < k_0 \leq k$, p_{k_0} is not below any node in C , as N is acyclic and r_m

is maximal under $\prec_{\mathcal{X}}$. Hence, there is a path P from $\rho(N)$ to p_{k_0} that does not contain any node in C . Since ℓ is a descendant of r_m , P can be extended into a path from $\rho(N)$ to ℓ that does not contain $\rho(C)$. This contradicts that $\rho(C)$ is visible on ℓ . Therefore, the parents of r_m are all in C .

(iv) It is derived from the fact that N is acyclic. \square

Time complexity for finding tree-node decomposition Let N be a binary reticulation-visible network. Since N is a DAG and has at most $8|\mathcal{L}(N)|$ nodes [6], we can determine the tree-node components using the breadth-first search technique in $O(|\mathcal{L}(N)|)$ time. Additionally, a topological ordering of its nodes can also be found in $O(|\mathcal{L}(N)|)$ time. Using such a topological ordering, we can derive a topological ordering for the big tree-node components. With this ordering, we can identify a lowest tree-node component described in Theorem 4.1(iv) in constant time.

For non-binary networks, the above process for determining the big tree-node components and a lowest one in $O(|\mathcal{V}(N)| + |\mathcal{E}(N)|)$ time.

We will use the decomposition theorem to develop fast algorithms for the TCP in Section 5. The theorem also seems to be very useful for studying the combinatorial aspects of networks. A network is galled if each reticulation node r has an ancestor u such that two internal-node disjoint paths exist from u to r in which all nodes except r are tree nodes. Galled networks are reticulation-visible [12].

Theorem 4.2 *For any arbitrary galled network N with n leaves, $|\mathcal{R}(N)| \leq 2(n - 1)$.*

Proof Let N be a galled network with n leaves. It is reticulation-visible [12]. We consider the tree-node components of N . Since the root of each tree-node component is either the network root or the unique child of a reticulation,

$$|\mathcal{R}(N)| = (\text{no. of tree-node components in } N) - 1. \quad (1)$$

We first show that N does not contain any cross reticulations. Suppose on the contrary N contains a cross reticulation r . By the definition of cross reticulation, the parents of r are in different tree-node components. Assume p_1 and p_2 are two parents of r in different tree-node components. Since N is acyclic, we may assume that p_1 is not below p_2 . Let C_{p_i} be the tree-node components containing p_i for $i = 1, 2$. We consider the parent r' of $\rho(C_{p_2})$. r' is a reticulation node. Furthermore, p_2 is below r' and hence r is also below r' . However, we can reach r from p_1 using a single edge without passing through r' , contradicting the Separation Lemma for galled networks [12, p. 163].

We have proved that N does not contain any cross reticulations. Therefore, all the tree-node components are connected in a tree structure. Precisely, if G is the graph whose nodes are the tree-node components in which a node X is connected to another Y by a directed edge if the tree-node components represented by them are separated by a reticulation node between them, G is then a rooted tree.

Consider a leaf l in G . If the tree-node component represented by l is not a single-leaf component in N , there is no reticulation node below it and thus it must contain a leaf of N . Therefore, G has at most n leaves and thus at most $2n - 1$ nodes. In other words, N contains at most $2n - 1$ tree-node components. By Eqn. (1), $|\mathcal{R}(N)| \leq 2(n - 1)$. \square

5 A Cubic-time Algorithm for the TCP

In this section, we first present a polynomial-time algorithm for the TCP in the case when the given reticulation-visible network is binary. Then, we describe how to modify the algorithm into one for non-binary networks.

5.1 An algorithm for binary networks

In this subsection, we assume the given network is *binary* in which a tree node has two children and a reticulation node has two parents. We remark that each internal node has two children in a phylogenetic tree.

Let N be a binary reticulation-visible network and T be a tree over the same leaves. A reticulation node in N is *inner* if its parents are all in the *same* tree-node component of N . It is called a *cross* reticulation otherwise.

By Theorem 4.1, there exists a “lowest” big tree-node component C below which there are only (if any) single-leaf components (Figure 3). We assume that C contains k network leaves, say $\ell_1, \ell_2, \dots, \ell_k$, and there are:

- m inner reticulations $\text{IR}(C) = \{r_1, r_2, \dots, r_m\}$, and
- n cross reticulations $\text{CR}(C) = \{r'_1, r'_2, \dots, r'_{m'}\}$

below C . Since C is a big tree-node components, it has two or more nodes, implying that $k + m + m' \geq 2$.

Let $\rho(C)$ denote the root of C . We further define:

$$L_C = \{\ell_1, \ell_2, \dots, \ell_k, c(r_1), c(r_2), \dots, c(r_m)\}. \quad (2)$$

By Theorem 4.1(iii)(b), $k + m \geq 1$ and so L_C is non-empty. Each path P from $\rho(N)$ to $c(r_i) \in L_C$ must contain r_i . Since the parents of r_i are all in C , P must contain $\rho(C)$. Hence, $\rho(C)$ is visible on each network leaf in L_C .

We select an $\ell \in L_C$. Since T has the same leaves as N , $\ell \in \mathcal{L}(T)$ and there is a unique path P_T from $\rho(T)$ to ℓ in T . Let:

$$P_T : v_1, v_2, \dots, v_t, v_{t+1}, \quad (3)$$

where $v_1 = \rho(T)$ and $v_{t+1} = \ell$. Then, $T - P_T$ is a union of t disjoint subtrees T_1, T_2, \dots, T_t , where T_i is the subtree rooted at the sibling of v_{i+1} for each $i = 1, 2, \dots, t$ (see Figure 2B). For the sake of convenience, we consider the single leaf ℓ as a subtree, written as T_{t+1} . We now define s_C as:

$$s_C = \min\{s \mid \mathcal{L}(T_s) \cap L_C \neq \emptyset\} \quad (4)$$

Since $\ell \in \mathcal{L}(T_{t+1}) \cap L_C$, s_C is well defined. In the example given in Figure 2, $s_C = 4$.

Proposition 5.1 *The index s_C can be computed in $O(|\mathcal{L}(N)|)$ time.*

Proof Since T is a binary tree with the same set of labeled leaves as the network N . T has $2|\mathcal{L}(N)| - 1$ nodes and $2|\mathcal{L}(N)| - 2$ edges. For each $x \in \mathcal{V}(T)$, we define a flag variable f_x to indicate whether the subtree below x contains a network leaf in L_C or not. We first traverse T in the post-order:

- For a leaf $x \in \mathcal{L}(T)$, $f_x = 1$ if $x \in L_C$ and 0 otherwise.
- For a non-leaf node x with children y and z , $f_x = \max\{f_y, f_z\}$.

Then, we compute s_C as $s_C = \min\{i \mid f_{\rho(T_i)} = 1\}$. Clearly, this algorithm correctly computes s_C in $O(|\mathcal{L}(T)|)$ time. \square

Proposition 5.2 *If N displays T , then $\mathcal{D}_T(v_{s_C})$ is displayed in $\mathcal{D}_N(\rho(C))$.*

Proof When $s_C = t + 1$, then the statement is trivial, as $\rho(C)$ is visible on ℓ and thus every path from the network root to ℓ must contain $\rho(C)$.

When $s_C < t + 1$, by the definition of s_C , there is a network leaf ℓ' in $\mathcal{L}(T_{s_C}) \cap L_C$ such that $\ell' \neq \ell$. If N displays T , T has a subdivision T' in N . Recall that $\rho(C)$ is visible on both ℓ and ℓ' . The paths from $\rho(T')$ to ℓ and to ℓ' in T' must both contain $\rho(C)$. Since T' is a tree, the lowest common ancestor $a(\ell, \ell')$ of ℓ and ℓ' is a descendant of $\rho(C)$ in T' and it is the node in T' that corresponds to v_{s_C} . Therefore, the subnetwork of T' below $a(\ell, \ell')$ is a subdivision of $\mathcal{D}_T(v_{s_C})$, that is, $\mathcal{D}_N(\rho(C))$ displays $\mathcal{D}_T(v_{s_C})$. \square

If N displays T , then C may display more than $\mathcal{D}_T(v_{s_C})$. In other words, it may display a subtree $\mathcal{D}_T(v_j)$ for some $j < s_C$. We define:

$$d_C = \min \{j \mid \mathcal{D}_T(v_j) \text{ is displayed in } \mathcal{D}_N(\rho(C))\} \quad (5)$$

In the example given in Figure 2, $d_C = 3$.

Proposition 5.3 *If N displays T , there must be a subdivision T'' of T in N such that the node (in T'') corresponding to v_{d_C} is in C .*

Proof Assume that N displays T via a subdivision T' of T . Let u be the node in T' that corresponds to v_{d_C} . Since $\rho(C)$ is visible on the leaf ℓ , $\rho(C)$ is in the unique path P from the root to ℓ in T' . If u is $\rho(C)$ or below it, we are done.

Assume that u is neither $\rho(C)$ nor below $\rho(C)$ in T' . Since ℓ is a network leaf below v_{d_C} in T , ℓ is also below u in T' . Hence, P must also contain u . Since u is not below $\rho(C)$, $\rho(C)$ must be below u in P .

On the other hand, by assumption, $\mathcal{D}_T(v_{d_C})$ is displayed in $\mathcal{D}_N(\rho(C))$. It has a subdivision T^* in $\mathcal{D}_N(\rho(C))$. Let v_{d_C} correspond to u' in T^* . It is not hard to see that u' is in the path from $\rho(C)$ to ℓ in T^* .

Let P' be the subpath from u to $\rho(C)$ of P and P'' be the path from $\rho(C)$ to u' in C . Since the subtree below u' in T^* and the subtree below u in T' has the same set of labeled leaves as the subtree below v_{d_C} in T ,

$$T' - \mathcal{D}_{T'}(u) + P' + P'' + \mathcal{D}_{T^*}(u')$$

is also a subdivision of T in N , in which v_{d_C} is mapped to u' in C . Here, $G + H$ is the graph with the same node set as G and the edge set being the union of $E(G)$ and $E(H)$ for graphs G and H such that $V(H) \subseteq V(G)$. \square

To compute d_C defined in Eqn.(5), we create a tree T_C from C by attaching two identical copies of the network leaf below each $r \in \text{IR}(C)$ to its parents in $p(r)$ in C and one copy of

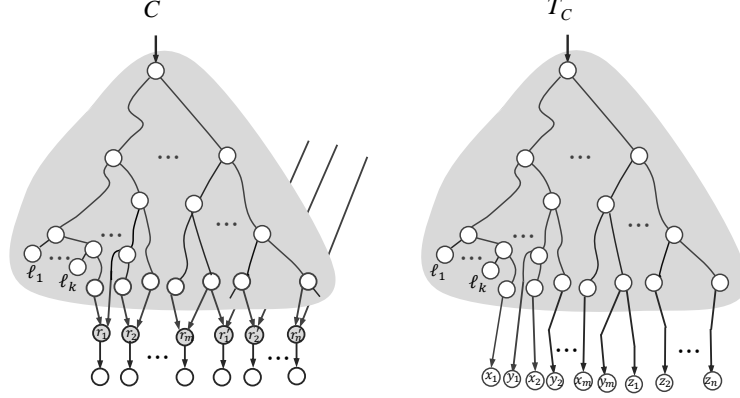


Figure 3: Illustration of a lowest tree-node component C in a binary reticulation-visible network and the corresponding tree T_C constructed for computing d_C in Proposition 5.4.

the network leaf below $r \in \text{CR}(C)$ to the parent in $p(r) \cap \mathcal{V}(C)$. That is, T_C has the node set:

$$\mathcal{V}(T_C) = \mathcal{V}(C) \cup \{x_r, y_r \mid r \in \text{IR}(C)\} \cup \{z_r \mid r \in \text{CR}(C)\}, \quad (6)$$

and the edge set

$$\begin{aligned} \mathcal{E}(T_C) = & \mathcal{E}(C) \cup \{(u_r, x_r), (v_r, y_r) \mid r \in \text{IR}(C) \text{ with } p(r) = \{u_r, v_r\}\} \\ & \cup \{(u_r, z_r) \mid r \in \text{CR}(C) \text{ with } \{u_r\} = p(r) \cap \mathcal{V}(C)\}, \end{aligned} \quad (7)$$

where x_r , y_r , and z_r are new leaves with the same label as $c(r)$ for each r in $\text{IR}(C)$ or $\text{CR}(C)$. T_C is illustrated in Figure 3.

Proposition 5.4 *There is a dynamic programming algorithm that takes T_C and T as input and outputs d_C defined in Eqn. (5) in $O(|\mathcal{V}(C)|^2|\mathcal{V}(T)|)$ time.*

Proof It is a special case of a problem studied in [22].

For each $r \in \text{IR}(C)$, T_C contains two leaves with the same label as $c(r)$. To detect whether or not $\mathcal{D}_T(v_j)$ is displayed in $\mathcal{D}_N(\rho(C))$, we have to consider which of these two leaves will be removed. Such leaves will be referred to the *ambiguous* leaves. We use $A(T_C)$ to denote the set of ambiguous leaves in T_C .

For each $r \in \text{CR}(C)$, T_C contains one leaf with the same label as $c(r)$. Similar to the case of ambiguous leaves, this leaf may be removed or kept. Such leaves are called *optional* leaves. We use $O(T_C)$ to denote the set of optional leaves in T_C .

Since each node in C is a tree node of degree 3 in N , T_C is a full binary tree with at most $2|\mathcal{V}(C)| + 1$ nodes.

For our purpose, we shall present a dynamic programming algorithm to compute the following set S_u of nodes in T :

$$S_u = \{x \in \mathcal{V}(T) \mid \mathcal{D}_{T_C}(u) \text{ displays } \mathcal{D}_T(x) \text{ where } u \text{ is mapped to } x\}$$

for each node u in T_C . Here, that $\mathcal{D}_{T_C}(u)$ displays $\mathcal{D}_T(x)$ means that $V_x \subseteq \mathcal{V}(T_C)$ exists such that $T_C - V_x$ is a subdivision of $\mathcal{D}_T(x)$. Since T_C is a tree, V_x consists of all the ambiguous or optional leaves that are in $\mathcal{D}_{T_C}(u)$ but not in $\mathcal{D}_T(x)$ and some ancestors of these leaves.

We introduce a boolean variable f_{ux} to indicate whether or not $\mathcal{D}_{T_C}(u)$ displays $\mathcal{D}_T(x)$ and a set variable M_{ux} to record those removed leaves if so. That is,

$$f_{ux} = \begin{cases} 1 & \text{if } \mathcal{D}_{T_C}(u) \text{ displays } \mathcal{D}_T(x), \\ 0 & \text{otherwise,} \end{cases} \quad (8)$$

and

$$M_{ux} = \mathcal{L}_{T_C}(u) \setminus \mathcal{L}_T(x) \quad (9)$$

if $f_{ux} = 1$, where $\mathcal{L}_Y(z)$ denotes the set of leaves below z in the tree Y .

When u is a leaf in T_C , we consider whether x is a leaf or not to compute f_{ux} .

If x is a leaf with the same label as u , then $\mathcal{D}_{T_C}(u)$ displays $\mathcal{D}_T(x)$ and thus we set $f_{ux} = 1$ and $M_{ux} = \emptyset$.

If x is a leaf and its label is different from the label of u , $\mathcal{D}_{T_C}(u)$ does not display $\mathcal{D}_T(x)$. In this case, $f_{ux} = 0$ and M_{ux} is undefined.

If x is not a leaf, it is trivial that $\mathcal{D}_{T_C}(u)$ does not display $\mathcal{D}_T(x)$. Hence, $f_{ux} = 0$ and M_{ux} is undefined.

When u is an internal node with children v and w in T_C , we consider similar cases. If x is a leaf, $\mathcal{D}_T(x)$ may or may not be displayed in $\mathcal{D}_{T_C}(u)$ if it is displayed below a child of u . If $\mathcal{D}_T(x)$ is displayed below v , it is also displayed at u only if every ambiguous leaf in M_{vx} is not below w and all the leaves below w are either ambiguous or optional. If $\mathcal{D}_T(x)$ is displayed below neither v nor w , it is not displayed at u . The remaining cases can be found in Table 1

Our dynamic programming algorithm recursively computes f_{ux} for each u and x by traversing both T_C and T in the post-order. For each u and x , we compute f_{ux} using the formulas listed in Table 1. Note that M_{ux} is a subset of $A(T_C) \cup O(T_C)$ and hence has at most $2|\mathcal{V}(C)|$ elements. Therefore, each recursive step takes $O(|\mathcal{V}(C)|)$ time. Because of this, the total time taken by the algorithm is $O(|\mathcal{V}(T)| \cdot |\mathcal{V}(C)|^2)$.

After we know the values of f_{ux} for every u in T_C and every x in T_c , we can compute d_C such that $\mathcal{D}_T(v_j)$ is displayed in $\mathcal{D}_N(\rho(C))$ as

$$d_C = \min_{1 \leq j \leq t+1} \{j \mid f_{uv_j} = 1 \text{ for some } u \in \mathcal{V}(T_C)\}.$$

□

$x \in \mathcal{L}(T)?$	f_{vx}	f_{wx}	f_{ux} and M_{ux}
Yes	1	1	(a.) $f_{ux} = \begin{cases} 1 & \text{if } M_{vx} \cap M_{wx} = \emptyset, \\ 0 & \text{otherwise.} \end{cases}$ $M_{ux} = M_{vx} \cup M_{wx} \cup \{x\} \text{ if } f_{ux} = 1$
	1	0	(b.) $f_{ux} = \begin{cases} 1 & \text{if } \mathcal{L}(\mathcal{D}_{T_C}(w)) \subseteq A(T_C) \cup O(T_C), \\ & \& M_{vx} \cap \mathcal{L}(\mathcal{D}_{T_C}(w)) = \emptyset, \\ 0 & \text{otherwise.} \end{cases}$ $M_{ux} = M_{vx} \cup \mathcal{L}(\mathcal{D}_{T_C}(w)) \text{ if } f_{ux} = 1$
	0	1	(c.) $f_{ux} = \begin{cases} 1 & \text{if } \mathcal{L}(\mathcal{D}_{T_C}(v)) \subseteq A(T_C) \cup O(T_C), \\ & \& M_{wx} \cap \mathcal{L}(\mathcal{D}_{T_C}(v)) = \emptyset, \\ 0 & \text{otherwise.} \end{cases}$ $M_{ux} = M_{wx} \cup \mathcal{L}(\mathcal{D}_{T_C}(v)) \text{ if } f_{ux} = 1$
	0	0	$f_{ux} = 0$
No. $c(x) = \{y, z\}$	1	(d.) 1	f_{ux} is defined same as the leaf case $M_{ux} = M_{vx} \cup M_{wx} \cup \mathcal{L}(\mathcal{D}_T(x)) \text{ if } f_{ux} = 1$
	1	0	(e.) same as the leaf case
	0	1	(f.) same as the leaf case
	0	0	(h.) $f_{ux} = \begin{cases} 1 & \text{if } f_{vy} = 1 \& f_{wz} = 1 \\ & \& M_{vy} \cap M_{wz} = \emptyset, \\ 1 & \text{if } f_{vz} = 1 \& f_{wy} = 1 \\ & \& M_{vz} \cap M_{wy} = \emptyset, \\ 0 & \text{otherwise.} \end{cases}$ $M_{ux} = \begin{cases} M_{vy} \cup M_{wz} & \text{if } f_{vy} = 1 \& f_{wz} = 1, \\ M_{vz} \cup M_{wy} & \text{if } f_{vz} = 1 \& f_{wy} = 1. \end{cases}$

Table 1: The recursive formulas on f_{ux} for different cases when u is an internal node in T_C .

Based on the facts presented above, we obtain the following algorithm for the TCP.

THE TCP ALGORITHM

Input: A reticulation-visible network N and a tree T , which are binary.

1. Decompose N into tree-node components: $C_1 \prec C_2 \prec \cdots \prec C_t$, where \prec is a topological order such that that no directed path from a node u in C_j to a node v in C_i exists if $j > i$;
 2. $N' \leftarrow N$ and $T' \leftarrow T$;
 3. **Repeat** unless (N' becomes a single node) {
 - 3.1. Select a lowest big tree-node component C ;
 - 3.2. Compute L_C in Eqn. (2) and select $\ell \in L_C$;
 - 3.3. Compute the path P_T from the root to ℓ in Eqn. (3);
 - 3.4. Determine the smallest index s_C defined by Eqn. (4);
 - 3.5. Determine the smallest index d_C defined by Eqn. (5);
 - 3.6. **If** ($s_C > d_C$), output “ N does not display T ”;
 - else** {
 - For each $r \in \text{CR}(C)$ {
 - if ($c(r) \notin \mathcal{D}_T(v_{d_C})$), delete (z, r) for $z \in p(r) \cap \mathcal{V}(C)$;
 - if ($c(r) \in \mathcal{D}_T(v_{d_C})$), delete (z, r) for $z \in p(r) \setminus \mathcal{V}(C)$;
 - Replace C (resp. $\mathcal{D}_T(v_{d_C})$) by a leaf ℓ_C in N' (resp. T');
 - Remove C from the list of tree-node components;
 - Update $\text{CR}(C')$ for the affected big tree-node components C'' ;
 - } /* end if */
 - } /* end repeat */
-

We now analyze the time complexity of the TCP ALGORITHM. Note that N has at most $8|\mathcal{L}(N)|$ nodes [6] and the input tree contains $2|\mathcal{L}(N)| - 1$ nodes. Step 1 can be done in $O(|\mathcal{L}(N)|)$ time if the breadth-first search is used.

Step 3 is a while-loop. During each execution of this step, the current network is obtained from the previous network by replacing the big tree-node component examined in the last execution with a new leaf node. Because of this, the modification done in the last two lines in Step 3.6 makes the tree decomposition of the current network available before the current execution. Hence, Step 3.1 takes a constant time. The time spent in Step 3.2 for each execution is linear in the sum of the numbers of the leaves in C and of the inner reticulations below C . Hence, the total time spent in Step 3.2 is $O(|\mathcal{L}(N)|)$, as each reticulation is examined twice at most.

By Proposition 5.1, the total time spent in Step 3.4 is $O(|\mathcal{L}(N)|^2)$. By Proposition 5.4, the total time spent in Step 3.5 is $\sum_i O(|\mathcal{V}(C_i)|^2 |\mathcal{L}(T)|)$, which is $O(|\mathcal{L}(N)|^3)$. The time spend in Step 3.6 for each execution is $O(|\mathcal{V}(C)|)$. Hence, the total time spent in Step 3.6 is $O(|\mathcal{L}(N)|)$. Taken altogether, the above facts imply that the TCP ALGORITHM takes $O(|\mathcal{L}(N)|^3)$ time, proving Theorem 3.1.

5.2 Generalization to non-binary networks

The algorithm in the last subsection can be easily modified into a polynomial time TCP algorithm for non-binary reticulation-visible networks in which tree nodes are of indegree 1 and outdegree greater than 1, whereas reticulation nodes are of indegree greater than 1 and outdegree 1. First, we have proved the decomposition theorem for arbitrary reticulation-visible networks. Second, the concepts of inner and cross reticulation remain the same. Third, Propositions 5.1-5.3 still hold. The only modification we have to make is on the definition of T_C , appearing in Step 3.5, and on the proof of Proposition 5.4. It can be done as follows.

Eqn. (6) and (7) now become

$$\begin{aligned} \mathcal{V}(T_C) &= \mathcal{V}(C) \\ &\cup \{x_r^{(i)} \mid r \in \text{IR}(C) \text{ \& } 1 \leq i \leq |p(r)|\} \\ &\cup \{z_r^{(i)} \mid r \in \text{CR}(C) \text{ having } k \text{ parents in } C \text{ \& } 1 \leq i \leq k\}, \end{aligned} \quad (10)$$

and the edge set

$$\begin{aligned} \mathcal{E}(T_C) &= \mathcal{E}(C) \\ &\cup \{(u_r^{(i)}, x_r^{(i)}) \mid r \in \text{IR}(C) \text{ with } p(r) = \{u_r^{(i)} \mid 1 \leq i \leq k\}\} \\ &\cup \{(u_r^{(i)}, z_r^{(i)}) \mid r \in \text{CR}(C) \text{ with } p(r) \cap \mathcal{V}(C) = \{u_r^{(i)} \mid 1 \leq i \leq k\}\}, \end{aligned} \quad (11)$$

where $x_r^{(i)}$, and $z_r^{(i)}$ are new leaves with the same label as $c(r)$ for each r in $\text{IR}(C)$ or $\text{CR}(C)$. We further define:

$$A_r = \{x_r^{(i)} \mid 1 \leq i \leq |p(r)|\}. \quad (12)$$

for $r \in \text{IR}(C)$.

We now describe how to compute f_{ux} defined in Eqn. (8) when u is a non-leaf node in N . (When u is a leaf, we can compute f_{ux} in the same way as in the case when N is binary.)

When x is a leaf in T , $f_{ux} = 0$ if $f_{vx} = 0$ for each $v \in c(u)$. Conversely, if $f_{v'x} = 1$ for some $f_{ux} = 1$ only if

- (i) $\mathcal{L}(\mathcal{D}_{T_C}(v)) \subseteq A(T_C) \cup O(T_C)$ for each $v \neq v'$ in $c(u)$, and
- (ii) $A_r \not\subseteq M_{v'x} \cup [\cup_{v \in c(u) \setminus \{v'\}} \mathcal{L}(\mathcal{D}_{T_C}(v))]$ for each $r \in \text{IR}(C)$, where $M_{v'x}$ is defined in Eqn. (9).

The reason for (i) is that if the display of $\mathcal{D}_T(x)$ is extended from the subtree rooted at v' to the subtree rooted at u , we have to delete the subtrees rooted at any other child of u . The reason for (ii) is that we cannot delete all the leaves added for each $r \in \text{IR}(C)$.

It is possible that $f_{vx} = 1$ for different children v of u . However, we would like to point out, whether the conditions (i) and (ii) hold or not is independent of which child is selected when it happens.

When x is not a leaf, we assume $c(x) = \{y, z\}$. Clearly, if $f_{vx} = 0$ for each $v \in c(u)$ and no v' and v'' exist in $c(u)$ such that $f_{v'y} = 1$ and $f_{v''z} = 1$, then $f_{ux} = 0$.

If $f_{v'x} = 1$ for some $v' \in c(u)$, we can determine whether or not $f_{ux} = 1$ in the same way as in the case when x is a leaf.

If $f_{v'y} = 1$ and $f_{v''z} = 1$ for $v', v'' \in c(u)$ such that $v' \neq v''$, $f_{ux} = 1$ only if

- (i) $\mathcal{L}(\mathcal{D}_{T_C}(v)) \subseteq A(T_C) \cup O(T_C)$ for each $v \in c(u)$ such that $v' \neq v \neq v''$, and
- (ii) $A_r \not\subseteq M_{v'x} \cup M_{v''x} \cup [\cup_{v \in c(u) \setminus \{v', v''\}} \mathcal{L}(\mathcal{D}_{T_C}(v))]$ for each $r \in \text{IR}(C)$.

Again, the two conditions are independent of which v' and v'' are selected.

To efficiently check the conditions (i) and (ii), we introduce some integer variables for each node. For each $r \in \text{IR}(C)$ and each node u in T_C , m_{ur} denotes the number of leaves in $\mathcal{L}(\mathcal{D}_{T_C}(u))$ that are in A_r ; m_{u0} denotes the number of non-ambiguous and non-optional leaves in $\mathcal{L}(\mathcal{D}_{T_C}(u))$. It is not hard to see that m_{u0} can be recursively computed using

$$m_{u0} = \begin{cases} 1 & \text{if } u \text{ is a leaf in neither } A(T_C) \text{ nor } O(T_C), \\ 0 & \text{if } u \text{ is a leaf in } A(T_C) \text{ or } O(T_C), \\ \sum_{v \in c(u)} m_{v0} & \text{if } u \text{ is a non-leaf node.} \end{cases} \quad (13)$$

Similary, m_{ur} can be updated as follows:

$$m_{ur} = \begin{cases} 1 & \text{if } u \text{ is a leaf in } A_r, \\ 0 & \text{if } u \text{ is a leaf not in } A_r, \\ \sum_{v \in c(u)} m_{vr} & \text{if } u \text{ is a non-leaf node.} \end{cases} \quad (14)$$

The subset relation in the condition (i) is equivalent to that $m_{v0} = 0$. Note that $\mathcal{L}(\mathcal{D}_{T_C}(u)) \cap A_r = [M_{v'x} \cup M_{v''x} \cup (\cup_{v \in c(u) \setminus \{v', v''\}} \mathcal{L}(\mathcal{D}_{T_C}(v)))] \cap A_r$ for each $r \in \text{IR}(C)$ such that its leaf child $c(r)$ is not in $\mathcal{L}(\mathcal{D}_T(x))$. As the condition (ii) is clearly true if $c(r)$ is in $\mathcal{L}(\mathcal{D}_T(x))$, it is equivalent to that $m_{ur} < |A_r|$ for each $r \in \text{IR}(C)$ such that $c(r)$ is not in $\mathcal{L}(\mathcal{D}_T(x))$. Thus, we can update f_{ux} using the formulas in Table 2.

Using Eqn. (13) and (14), we can pre-compute m_{u0} and m_{ur} for all $r \in \text{IR}(C)$ in $|\mathcal{E}(T_C)| \cdot (|\text{IR}(C)| + 1)$ time.

When f_{ux} is updated, we need to check whether or not $f_{vx} = 1$ and $f_{vy} = 1$ for each $y \in c(x)$ and each child $v \in c(u)$. This can be done in $O(|c(u)|)$ time. Similarly, the condition (i) is independent of x and can be checked in $O(|c(u)|)$ time; the condition (ii) can be checked in $O(|\text{IR}(C)|)$ time. Hence, for all nodes x in T , the run time for updating f_{ux} in T_C takes $O(\sum_{u \in \mathcal{V}(T_C)} (|c(u)| + |\text{IR}(C)|)) = O(|\mathcal{E}(T_C)| + |\text{IR}(C)| \cdot |\mathcal{V}(T_C)|)$ time. This implies that the run time on T_C for all nodes in T is $O(|\mathcal{V}(T)| \cdot [|\mathcal{E}(T_C)| + |\text{IR}(C)| \cdot |\mathcal{V}(T_C)|])$ time.

Therefore, the total run time for determining whether or not T is displayed in N is $O(|\mathcal{V}(T)| \cdot [|\mathcal{E}(N)| + |\mathcal{R}(N)| \cdot |\mathcal{E}(N)|]) = O(|\mathcal{V}(T)| \cdot |\mathcal{E}(N)| \cdot |\mathcal{R}(N)|)$ time. In general, $|\mathcal{E}(N)|$ is not bounded by any function linear in the number of leaves in an arbitrary network.

6 A Linear-time Algorithm for the CCP

As another application of the Decomposition Theorem, we shall design a linear-time algorithm for the CCP. We first present a desired algorithm for binary reticulation-visible networks and then generalize it to non-binary networks.

6.1 Algorithm for binary networks

Given a binary reticulation-visible network N and a subset $B \subseteq \mathcal{L}(N)$, the goal is to determine whether or not B is a cluster of some node in a tree displayed by N .

$x \in \mathcal{L}(T)?$	f_{ux} and M_{ux}
Yes	<p>Case 1: $f_{vx} = 0$ for each $v \in c(u)$ $f_{ux} = 0$;</p> <p>Case 2: $f_{v'x} = 1$ for some $v' \in c(u)$ If (i) $m_{v0} = 0$ for each $v \neq v'$ in $c(u)$, and (ii) $m_{ur} < A_r$ for each $r \in \text{IR}(C)$ such that $A_r \cap \mathcal{L}(\mathcal{D}_T(x)) = \emptyset$, { $f_{ux} = 1$; } else $f_{ux} = 0$;</p>
No. $c(x) = \{y, z\}$	<p>Case 1: $f_{vx} = 0$ for any $v \in c(u)$, and no v' and v'' in $c(u)$ exist such that $f_{v'y} = 1$ and $f_{v''z} = 1$; $f_{ux} = 0$;</p> <p>Case 2: $f_{v'x} = 1$ for some $v' \in c(u)$ Use the same update rule as in the case 2 when x is a leaf</p> <p>Case 3: $f_{v'y} = 1$ and $f_{v''z} = 1$ for some $v' \neq v''$ in $c(u)$ If (i) $m_{v0} = 0$ for each $v \in c(u)$ such that $v' \neq v \neq v''$, and (ii) $m_{ur} < A_r$ for each $r \in \text{IR}(C)$ such that $A_r \cap \mathcal{L}(\mathcal{D}_T(x)) = \emptyset$, { $f_{ux} = 1$; } else $f_{ux} = 0$;</p>

Table 2: The update rules for computing f_{ux} for a node u in an arbitrary network.

Assume N has t big tree-node components C_1, C_2, \dots, C_t . Consider a lowest big tree-node component C . We use the same notation as in Section 5: L_C is defined in Eqn. (2); $\rho(C)$ denotes the root of C ; $\text{IR}(C)$ and $\text{CR}(C)$ denote the set of inner and cross reticulations below C , respectively. We also set $\bar{B} = \mathcal{L}(N) \setminus B$.

When $L_C \cap B \neq \emptyset$ and $L_C \cap \bar{B} \neq \emptyset$, L_C contains ℓ_1 and ℓ_2 such that $\ell_1 \in B$, but $\ell_2 \notin B$. If B is the cluster of a node z in a subtree T' of N , z is in the unique path P from $\rho(T')$ ($= \rho(N)$) to ℓ_1 in T' .

Assume z is between $\rho(N)$ and $\rho(C)$ in P , no matter which incoming edge is contained in T' for each $r \in \text{IR}(C)$, ℓ_2 is below $\rho(C)$, as $\rho(C)$ is visible on ℓ_2 . This implies that ℓ_2 is below z and thus in B , a contradiction. Therefore, if B is a soft cluster, it must be a soft cluster of a node in C .

When $L_C \cap \bar{B} = \emptyset$ (that is, $L_C \subseteq B$), we define

$$X = \{r \in \text{CR}(C) \mid c(r) \notin B\}. \quad (15)$$

Construct a subtree T' of $\mathcal{D}_N(\rho(C))$ by deleting:

- all but one of the incoming edges for each $r \in \text{IR}(C)$,
- all incoming edges but one with a tail not in C for each $r \in X$, and
- all incoming edges but one with a tail in C for each $r \in \text{CR}(C) \setminus X$.

We then define

$$\hat{B} = L_C \cup \{c(r) \mid r \in \text{CR}(C) \setminus X\}. \quad (16)$$

It is not hard to see that \hat{B} is the cluster of the root of T' such that $\hat{B} = B \cap \mathcal{L}(\mathcal{D}_N(\rho(C))) \subseteq B$. Hence, if $B = \hat{B}$, then B is a cluster contained in $\mathcal{D}_N(\rho(C))$. If $B \neq \hat{B}$, we reconstruct N' from N by:

- removing all the edges in $\{(u, r) \in \mathcal{E}(N) \mid r \in X, u \in \mathcal{V}(C)\}$,
- removing all the edges in $\{(u, r) \in \mathcal{E}(N) \mid r \in \text{IR}(C) \cup \text{CR}(C) \setminus X, u \notin \mathcal{V}(C)\}$,
- removing all but one of edges in $\{(u, r) \in \mathcal{E}(N) \mid r \in \text{IR}(C) \cup \text{CR}(C) \setminus X, u \in \mathcal{V}(C)\}$, and
- replacing $\mathcal{D}_N(\rho(C))$ by a new leaf ℓ_C .

and set $B' = \{\ell_C\} \cup B \setminus \hat{B}$. We have the following fact.

Proposition 6.1 *If $L_C \cap \bar{B} = \emptyset$, B is contained in N if and only if B' is contained in N' .*

Proof Recall that $B' = (B \cup \{\ell_C\}) \setminus \hat{B}$. If B' is the cluster of a node z in a tree T'' displayed in N' . When N' was reconstructed, ℓ_C replaced the subtree T' rooted at $\rho(C)$ whose leaves are \hat{B} ; so if we re-expand ℓ_C into T' , the cluster of z in N becomes $(B \setminus \hat{B}) \cup \hat{B} = B$, thus B is contained in N .

Assume B is the cluster of a node z in a subtree T displayed in N . Let E be the set of edges entering the reticulations nodes such that $T = N - E$. Since $B \neq \hat{B} = B \cap \mathcal{L}(\mathcal{D}_N(\rho(C)))$, there is a leaf $\bar{\ell} \in B$ not below $\rho(C)$. Since $\bar{\ell}$ is below z in T , z must be above $\rho(C)$ in T .

Consider a reticulation node $r \in \text{CR}(C) \setminus X$. Since $c(r)$ is a leaf in B , it is a leaf below z in T . By definition of cross reticulation, r has at least one parent in C . Let (p_C, r) be an edge such that $p_C \in C$. Note that all but one of that incoming edges of r are in E . Define

$$E' = [E \setminus \{(p_C, r) \mid r \in \text{CR}(C) \setminus X\}] \cup \{(p, r) \in \mathcal{E}(N) \mid r \in \text{CR}(C) \setminus X \text{ \& } p \notin \mathcal{V}(C)\}$$

. It is not hard to see that (p_C, r) is the unique incoming edge of r not in E' for each $r \notin X$.

Let $T' = N - E'$. It is easy to see that the cluster of z is equal to B and \hat{B} is the cluster of $\rho(C)$ in T' . Therefore, if we contract the subtree below $\rho(C)$ into a single leaf ℓ_C , the cluster of z becomes $B \cup \{\ell_C\} \setminus \hat{B}$, which is B' . Therefore, B' is contained in N' . \square

When $B \cap L_C = \emptyset$, B may or may not be contained in $\mathcal{D}_N(\rho(C))$. If it is not, we use X defined in Eqn. (15) to reconstruct N' from N by:

- removing all the edges in $\{(u, r) \in \mathcal{E}(N) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \notin B, u \notin \mathcal{V}(C)\}$,
- removing all the edges in $\{(u, r) \in \mathcal{E}(N) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \in B, u \in \mathcal{V}(C)\}$, and
- replacing $\mathcal{D}_N(\rho(C))$ by a new leaf ℓ_C .

Similar to the last case, we have the following fact.

Proposition 6.2 *If B is not in $\mathcal{D}_N(\rho(C))$ and $L_C \cap B = \emptyset$, it is a soft cluster in N if and only if B is a soft cluster in N' .*

Proof N' is a subnetwork of N . If B is a soft cluster in N' , it is a soft cluster in N .

Conversely, assume B is the cluster of a node z in a subtree T of N . Let E be the set of reticulation edges such that $T = N - E$. By assumption, B is not contained in $\mathcal{D}_N(\rho(C))$. Since $\rho(C)$ is visible on all leaves in L_C , $\rho(C)$ is not below z in T' . Therefore, $\rho(C)$ and z do not have ancestral relationship.

Consider a reticulation $r \in \text{CR}(C)$. Since r is a cross reticulation, it has a parent p_r in C . If $c(r) \in B$, $c(r)$ is a leaf below z in T and thus the unique incoming edge not in E has a tail not in C . If $c(r) \notin B$, the unique incoming edge not in E may or may not have a tail in C .

We define:

$$E' = (E \cup \{(p, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \notin B, p \notin C\}) \setminus \{(p_r, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \notin B\}.$$

Note that (p_C, r) is the unique incoming edge of r not in E' for each $r \in \text{CR}(C)$ such that $c(r) \notin B$. Let $T' = N - E'$. It is easy to see that the cluster of z in T' remains the same as the cluster of z in T , which is equal to B . If we contract $\mathcal{D}_{T'}(\rho(C))$ into a single leaf ℓ_C , T' is a subtree of N' , implying that B is a soft cluster in N' . \square

We next show that whether or not B is in C can be determined in linear time.

Proposition 6.3 *Let T_C be a subtree constructed from C in Eqn.(6) and (7). An algorithm exists that takes T_C and B as inputs and determines whether or not B is a soft cluster in C in $O(|\mathcal{E}(T_C)|)$ time.*

Proof First, we check whether or not each of the leaves in B is below $\rho(C)$. If $B \not\subseteq \mathcal{L}(\mathcal{D}_N(\rho(C)))$, B is not a soft cluster in $\mathcal{D}_N(\rho(C))$. We assume that $|B| \geq 2$ and all its leaves are found below $\rho(C)$.

Assume B is a cluster of a node v in a subtree T of $\mathcal{D}_N(\rho(C))$. Clearly, any network leaf in C is not below v if it is not in B . For each $r \in \text{IR}(C)$, $p' \in p(r)$ exists such that (p', r) was removed. If $c(r) \notin B$, the parent of r other than p' must not be below v . Since B is not singleton, v is an internal node in T_C . Taken together, these facts imply that v satisfies the following properties:

- (i) Every leaf in B is below v .
- (ii) if a leaf below v is neither ambiguous nor optional, it must be in B .
- (iii) If the ambiguous leaves introduced for a $r \in \text{IR}(C)$ are both below v , then $c(r) \in B$.

Conversely, if an internal node v of T_C satisfies the above three properties, we can then construct a subtree T of N in which B is the cluster of v as follows:

- For each $r \in \text{IR}(C) \cup \text{CR}(C)$ below v , if it has a parent p_1 below v and another parent p_2 not below v , remove (p_2, r) if $c(r)$ is in B and remove (p_1, r) otherwise.
- For any other reticulation node not below v , choose an arbitrary incoming edge to remove.

It is easy to verify that B is a cluster of v in the resulting tree.

Assume B is a cluster of an internal node v in $\mathcal{D}_N(\rho(C))$ and $\ell \in B$. If ℓ is not the child of an inner reticulation node below C , then v is contained in the path from $\rho(C)$ to ℓ in T_C .

Otherwise, v is contained in the path from $\rho(C)$ to one of the ambiguous leaves defined for ℓ in T_C .

Based on the above facts, we obtain ALGORITHM 1 (Table 3) to determine whether B is a cluster in C .

The correctness of the algorithm follows from the following facts. When the algorithm stops with answer “No” during the traversal of the subtree branching off at u in the path from $\rho(T_C)$ to the leaf x . It means that two ambiguous copies of a leaf not in B have been seen in the subtree below u . This implies that for any descendant w of u , not all leaves in B have been seen below w and for u and each of its ancestor, some leaf not in B has two ambiguous copies below it. Hence, no node exists in the path from the root to x in T_C that satisfies the properties (i)-(iii). When the algorithm exists at Step 4, B is clearly not a soft cluster in C .

When the algorithm stops with answer “Yes” at u inside Step 3.4, u is the lowest node satisfying the three properties. Hence, B is a soft cluster in C .

Next, we analyze the complexity of ALGORITHM 1. Step 1 and Step 2 can be done in $O(|\mathcal{L}(T_C)|)$ time. Since there are at most two leaves with that same label as ℓ in T_C , outer

ALGORITHM 1

Input: T_C and a subset B of leaves in $\mathcal{D}_N(\rho(C))$;

1. If $|B| = 1$, output “Yes” and exit;
 2. Set $k = |B|$ and $m = |\mathcal{L}(\mathcal{D}_N(\rho(C)))| - k$;
 Set a k -tuple $Y[1..k]$; /* record if a leaf in B has been seen */
 Set a m -tuple $Z[1..m]$;
 /*Use Z to record the copies of $\ell \notin B$ have not been seen so far */
 3. Select $\ell \in B$.
for each leaf x in T_C that has the same label as ℓ {
 3.1 $u = x$; $f = 1$; /* f is the no. of leaves in B have been seen so far */
 3.2 For each i from 1 to k , $Y[i] = 0$;
 3.3 For each i from 1 to m
 if (the i^{th} leaf $\ell' \notin B$ is ambiguous or optional) $Z[i] = 2$ else $Z[i] = 1$;
 3.4 **Repeat** while $u \neq \rho(C)$ {
 $v' = u$; $v'' = (\text{the sibling of } u)$; $u = p(u)$;
 for each ℓ' in the subtree { /* Traverse the subtree T_C rooted at v'' */
 if ($\ell' \in B$ having rank j) & ($Y[j] == 0$) { $Y[j] = 1$; $f = f + 1$ };
 if ($\ell' \notin B$ having rank j)
 $Z[j] = Z[j] - 1$; if ($Z[j] == 0$) **stop** Step 3.4;
 } /* end for */
 if ($f == |B|$) output “Yes” and **exit**;
 } /* end repeat */
 } /* end the outer for */
 4. output “No” and **exit**;
-

Table 3: An algorithm to decide whether a leaf subset B is a soft cluster in C .

for-loop will execute twice at most. At each execution of the for-loop, Steps 3.1-3.3 take $O(|\mathcal{L}(T_C)|)$ time. In Step 3.4, we may traverse different subtree of T_C that branch off at a node in the path from the root of T_C to x , so the total running time for Step 3.4 is $O(|\mathcal{E}(T_C)|)$. Hence, the algorithm runs in $O(|\mathcal{E}(T_C)| + |\mathcal{L}(T_C)|) = O(|\mathcal{V}(C)|)$, as $|\mathcal{E}(T_C)| \leq 3|\mathcal{V}(C)|$ in a binary network. \square

Taking all the above facts together, we are able to give a linear time algorithm for the CCP.

THE CCP ALGORITHM

Input: A binary network N and a subset $B \subseteq \mathcal{L}(N)$;

1. Compute the big tree-node components sorted in a topological order:
 $C_1 \prec C_2 \prec \cdots \prec C_t$;
 2. **for** $k = 1$ **to** t **do** {
 - 2.1. Set $C = C_k$; compute $L := L_{C_k}$ defined in Eqn. (1);
 - 2.2. $Y := (\text{Is } B \text{ contained in } \mathcal{D}_N(\rho(C)))?$;
 - 2.3. **if** ($Y == 1$) output “Yes” and **exit**;
 - 2.4. **if** ($Y == 0$) {
 - $\bar{B} := \mathcal{L}(N) \setminus B$;
 - if** ($L \cap \bar{B} \neq \emptyset \ \& \ B \cap L \neq \emptyset$) output “No” and **exit**;
 - if** ($B \cap L == \emptyset$) {
 - Remove edges in $\{(u, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \notin B, u \notin C\}$;
 - Remove edges in $\{(u, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \in B, u \in C\}$;
 - if** ($\bar{B} \cap L == \emptyset$) {
 - Remove edges in $\{(u, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \notin B, u \in C\}$;
 - Remove edges in $\{(u, r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \in B, u \notin C\}$;
 - $B := (B \cup \{\ell_C\}) \setminus (L \cup \{c(r) \mid r \in \text{CR}(C) \text{ s.t. } c(r) \in B\})$;
 - Replace $\mathcal{D}_N(\rho(C))$ by a leaf ℓ_C ;
 - Remove C from the list of big tree-node components;
 - Update $\text{CR}(C')$ for affected big tree-node components C' ;
- } /* for */
-

The obtained CCP algorithm runs in linear time. Step 1 takes $O(|\mathcal{V}(N)|) = O(|\mathcal{L}(N)|)$ time, as N is binary. Step 2 is a for-loop that runs t times. Since the total number of the network leaves in C_k and the reticulation nodes below C_k is at most $3|\mathcal{V}(C_k)|$, Step 2.1 takes $O(|\mathcal{V}(C_k)|)$ time for each execution. In Step 2.2, the linear-time ALGORITHM 1 is called to compute Y in $O(|\mathcal{V}(C_k)|)$ time. Obviously, Step 2.3 takes constant time. To implement Step 2.4 in linear time, we need to use an array A to indicate whether a network leaf is in B or not. A can be constructed in $O(|\mathcal{L}(N)|)$ time. With A , each conditional clause in Step 2.4 can be determined in $|L|$ time, which is at most $O(|\mathcal{V}(C_k)|)$. Since the total number of inner

and cross reticulations is at most $2|\mathcal{V}(C_k)|$, each line of Step 2.4 takes at most $O(|\mathcal{V}(C_k)|)$ time. Hence, Step 2.4 still takes $O(|\mathcal{V}(C_k)|)$ time. Taking all these together, we have that the total time taken by Step 2 is $\sum_{1 \leq k \leq t} O(|\mathcal{V}(C_k)|) = O(|\mathcal{V}(N)|) = O(|\mathcal{L}(N)|)$. Therefore, Theorem 3.2 is proved.

6.2 Generalization of the CCP algorithm to non-binary networks

Propositions 6.1 and 6.2 have been proved for non-binary reticulation-visible networks. The straightforward generalization of ALGORITHM 1 does not give a linear-time algorithm for determining whether a subset B of leaves is a soft cluster in $\mathcal{D}_N(\rho(C))$ for non-binary networks, as the outer for-loop in Step 3.4 will run k times if T_C contains k ambiguous/optional leaves that have the same label as the selected leaf in B . However, it is widely known that the lowest common ancestor (lca) of any two nodes in a tree can be computed in $O(1)$ after a linear-time pre-processing. In the rest of this subsection, we will use this result to prove Proposition 6.3 for non-binary networks.

Given a non-binary reticulation-visible network N and a $B \subseteq \mathcal{L}(N)$ such that $|B| > 1$, We work on a lowest big tree-node component C of N . Let T_C be the tree defined in Eqn. (10) and (11). For each $r \in \text{IR}(C)$, A_r denotes the set of ambiguous leaves defined in Eqn. (12) and $\text{lca}(r)$ denotes the lca of the leaves in A_r .

Proposition 6.4 *All the nodes in $V_{\text{lca}} = \{\text{lca}(r) \mid r \in \text{IR}(C)\}$ can be computed in $O(|\mathcal{E}(N)|)$ time.*

Proof We first pre-process T_C in $O(|\mathcal{E}(T_C)|)$ time so that for any two nodes u and v in T_C , $\text{lca}(u, v)$ can be found in $O(1)$ time [1, 10].

Initially, each lca node is undefined. We visit all leaves in T_C in a depth-first manner. When visiting a leaf ℓ that is ambiguous and added for $r \in \text{IR}(C)$, we set $\text{lca}(r) = \ell$ if $\text{lca}(r)$ is undefined, and $\text{lca}(r) = \text{lca}(\text{lca}(r), \ell)$ otherwise. Since each lca operation takes $O(1)$ time, the whole process takes $O(|\mathcal{E}(N)|)$ time. \square

Proposition 6.5 (i) *Let ℓ be a leaf in T_C that is neither ambiguous nor optional. If $\ell \notin B$, B is not a soft cluster of any node u in the path from $\rho(C)$ to ℓ in N .*

(ii) *For each $r \in \text{IR}(C)$ such that $c(r) \notin B$, B is not a soft cluster of any u in the path from $\rho(C)$ to $\text{lca}(r)$ inclusively in N .*

Proof (i) Since ℓ is neither ambiguous nor optional, all the nodes in the path from $\rho(C)$ to ℓ appears in any subtree T of N . Since $\ell \notin B$, so, the cluster of each node in the path is not equal to B .

(ii) For an inner reticulation node r below C , A_r contains at least two ambiguous leaves and thus $\text{lca}(r)$ is an internal node in C . Any subtree T of N contains exactly one incoming edge of r below $\text{lca}(r)$. Thus, the cluster of each node u in the path from $\rho(C)$ to $\text{lca}(r)$ in T must contain $c(r)$ and hence is not equal to B . \square

Let T_{lca} be the spanning subtree of T_C over $\{\ell \in \mathcal{L}(T_C) \mid \ell \notin A(T_C) \cup O(T_C)\} \cup V_{\text{lca}} \cup \{\rho(C)\}$, where $A(T_C)$ and $O(T_C)$ are the set of ambiguous and optional leaves in T_C , respectively. Clearly, T_{lca} is rooted at $\rho(C)$. We further define $V_{\text{max}} = \{v \in \mathcal{V}(T_C) \mid v \notin \mathcal{V}(T_{\text{lca}}) \text{ and } p(v) \in \mathcal{V}(T_{\text{lca}})\}$.

Proposition 6.6 *B is a soft cluster in $\mathcal{D}_N(\rho(C))$ if and only if a node $v \in V_{\max}$ exists such that for each $\ell \in B$ there is a leaf below v with the same label as ℓ .*

Proof Assume B is a soft cluster of a node u in $\mathcal{D}_N(\rho(C))$. By Proposition 6.5, u is not in T_{lca} and thus it is below some $v \in V_{\max}$. For any $\ell \in B$, u and hence v has a leaf descendant having the same label as ℓ .

Let $v \in V_{\max}$ satisfy the property that for each $\ell \in B$, there is a leaf ℓ' having the same label as ℓ . For each $x \in \text{IR}(C)$ such that $c(x) \notin B$, by the definition of V_{\max} , A_x contains an ambiguous leaf not below v . For this x , we select a parent p'_x of r not below v in C .

For each $y \in \text{IR}(C)$ such that $c(y) \in B$, we select a parent p''_y below v .

For each $r \in \text{CR}(C)$ such that $c(r) \in B$, we select a parent p_r below v .

Set

$$\begin{aligned} E = & \{(p, r) \in \mathcal{E}(N) \mid p \in \mathcal{V}(C), r \in A(T_C) \cup O(T_C)\} \\ & - \{(p'_x, x) \mid x \in \text{IR}(C) \text{ such that } c(x) \notin B\} \\ & - \{(p''_y, y) \mid y \in \text{IR}(C) \text{ such that } c(r) \in B\} \\ & - \{(p, r) \mid r \in \text{CR}(C) \text{ such that } c(r) \in B\} \end{aligned}$$

Then, $\mathcal{D}_N(\rho(C)) - E$ is a subtree in which B is the cluster of v . It is not hard to see that $\mathcal{D}_N(\rho(C)) - E$ can be extended into a subtree of N . \square

Taken together, the above facts imply ALGORITHM 2 for determining whether a leaf subset is a soft cluster in a lowest big tree-node component or not, presented in Table 4.

The correctness of the ALGORITHM 2 follows from Propositions 6.5 and 6.6. Step 1 takes constant time. Step 2 can be done in $O(\sum_{u \in \mathcal{V}(C)} |c(u)|)$ time. Step 3 takes $O(|\mathcal{E}(T_C)|)$ time (see [10]). By Proposition 6.4, Step 4 can be done in $O(|\mathcal{E}(T_C)|)$ time.

ALGORITHM 2

Input: T_C and a subset B of leaves in $\mathcal{D}_N(\rho(C))$;

1. If $|B| == 1$, output “Yes” and **exit**;
 2. Construct T_C defined in Eqn. (10) and (11);
 3. Pre-process T_C so that the lca of any two nodes can be found in $O(1)$ time;
 4. Traverse the leaves in T_C to compute the nodes in V_{lca} ;
 5. For each leaf $\ell \notin A(C) \cup O(C)$ such that $\ell \notin B$
 mark the nodes in the path from $\rho(T_C)$ to it;
 For each $r \in \text{IR}(C)$ such that $c(r) \notin B$
 mark the nodes in the path from $\rho(T_C)$ to $\text{lca}(r)$ inclusively;
 6. Traverse the nodes u in T_C to compute the nodes in V_{\max} :
 check if u is unmarked and its parent is marked in Step 5 when visiting u ;
 7. For each node $u \in V_{\max}$ {
 7.1 Check whether or not all leaves in B are below u ;
 7.2 Output “Yes” and **exit** if so;
 8. Output “No” and **exit**;
-

Table 4: An algorithm to decide whether B is a soft cluster in C in the non-binary case.

Two paths from $\rho(T_C)$ to nodes in V_{lca} may have a common subpath starting at the root. We mark the nodes in each of these paths in a bottom-up manner: whenever we reach a marked node, we stop the marking process in the current path. In this way, each marked node is visited twice at most and hence Step 5 can be executed in $O(|\mathcal{E}(T_C)|)$ time.

Obviously, Step 6 takes $O(|\mathcal{E}(T_C)|)$ time. For each node u , Step 7.1 takes $O(|\mathcal{E}(\mathcal{D}_{T_C}(u))|)$ time. Since all the examined subtrees are disjoint, the total time taken by Step 7.1 is $O(|\mathcal{E}(T_C)|)$ time.

Taken together, these facts imply that ALGORITHM 2 is a line-time algorithm. Plugging ALGORITHM 2 into Step 2.2 in the CCP algorithm, we can solve the CCP in linear time.

7 Conclusion

Our algorithms are designed using a powerful decomposition theorem. The theorem holds for arbitrary reticulation-visible networks. We are very interested in exploring its applications in the estimate of the size of a network having a visibility property and designs of algorithms for reconstructing reticulation-visible networks from gene trees or gene sequences. Another interesting problem is how to determine whether two networks display the same set of binary trees in polynomial time. A solution for this is definitely valuable in phylogenetics.

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